

Predation by phytoseiid mites on *Tetranychus lintearius* (Acari: Tetranychidae), an established weed biological control agent of gorse (*Ulex europaeus*)

P.D. Pratt,^{a,*} E.M. Coombs,^b and B.A. Croft^c

^a USDA/ARS Invasive Plant Research Laboratory, 3205 College Avenue, Fort Lauderdale, FL 33314, USA

^b Biological Control of Weeds, Oregon Department of Agriculture, 635 Capitol St. NE, Salem, OR 97301-2532, USA

^c Oregon State University, Department of Entomology, 2046 Cordley Hall, Corvallis, OR 97331, USA

Received 26 December 2001; accepted 16 July 2002

Abstract

Development of trophic relationships among introduced biological control agents and native (or introduced) parasitoids, predators, or pathogens can interfere with successful establishment, spread, and ecological impact on the target pest. For the introduced weed biological control agent *Tetranychus lintearius* (Dufor), we assessed predator acquisition, the ability of these predators to survive and reproduce when held with the weed biological control agent, and their impacts on agent populations. Surveys of *T. lintearius* (spider mite) colonies demonstrated that this biological control agent of gorse, *Ulex europaeus* L., has acquired generalist and specialist feeding predatory mites in its adventive range but association alone is insufficient evidence to conclude that these mites are negatively affecting the weed biological control agent. Predation bioassays demonstrated that all predatory mites tested can feed, survive, and reproduce when held with *T. lintearius* lending evidence to the interference hypothesis. The number of spider mite colonies and volume of gorse foliage colonized were higher when the introduced predatory mite *Phytoseiulus persimilis* Athias–Henriot was excluded from plots, indicating these mites are suppressing *T. lintearius* populations. We report the predation of *T. lintearius* by a complex of predatory mites that are routinely used for biological control of spider mites in agricultural systems. Published by Elsevier Science (USA).

Keywords: *Tetranychus lintearius*; *Ulex europaeus*; Biotic resistance; Interference; Predatory mite; Biocontrol; Nontarget effects

1. Introduction

Classical weed biological control involves reuniting an invasive plant with coevolved natural enemies from its native range. Biological control theory suggests that the introduction of a natural enemy in the absence of higher trophic levels (i.e., parasites, predators, and pathogens) will facilitate exponential growth of the agent in response to the target pest (McEvoy and Coombs, 1999). Therefore, prior to release, particular emphasis is placed on ensuring that parasites, predators, and pathogens of the biological control agent are not inadvertently introduced into the new habitat (Fisher

and Andres, 1999). Accidental introduction of natural enemies from these higher trophic levels into the weed's adventive range may limit the success of biological control (Beirne, 1975).

Acquisition of natural enemies that are endemic to the weed's adventive range may also influence successful establishment, spread, and impact of classical weed biological control agents (Goeden and Louda, 1976). For example, the spider mite *Tetranychus lintearius* (Dufor) was introduced into New Zealand in 1989 as a biological control agent of the invasive weed gorse, *Ulex europaeus* L. (Fabaceae) (Hill et al., 1991; Hill and Stone, 1985). Although successfully established and widely distributed, gorse spider mite populations rarely reached sufficient densities to severely damage the target weed (Rees and Hill, 2001). Subsequent studies suggested that the endemic coccinellid, *Stethorus bifidus* (Kapur) (Coleop-

* Corresponding author. Fax: 1-954-476-9169.

E-mail address: prattp@saa.ars.usda.gov (P.D. Pratt).

tera: Coccinellidae), was a major mortality factor of *T. lintearius* and limited biological control success of this spider mite (Peterson, 1993; Peterson et al., 1994). These findings lend support to the opinion that natural enemies can suppress spider mites below outbreak levels in most, if not all, natural systems (Croft, 1990; Helle and Sabelis, 1985; Walter and Proctor, 1999).

Gorse is also an invasive weed in coastal regions of North America, where it threatens sensitive habitats and limits access to public lands (Rees et al., 1996). Invasion of this weed has resulted in displacement of native plants (i.e., *Lycopodium inundatum* L.) and animals (i.e., *Speyeria zerene* var. *hippolyta* (Edwards)). Five years after its release in New Zealand, *T. lintearius* was also introduced into gorse-infested regions of Oregon, USA. In contrast to previous introductions, *T. lintearius* colonies reached high population densities shortly after release, dispersed widely, and caused severe, localized plant damage to *U. europaeus* (E.M. Coombs, unpublished data). These differences in population dynamics caused us to question whether *T. lintearius* had acquired native natural enemies of spider mites in the coastal regions of Oregon and, if so, what impact were they having on the biological control agent. Among natural enemies of spider mites, predaceous arthropods are the most common and specific, with pathogens being rare and parasitoids nonexistent (Helle and Sabelis, 1985; Van der Geest et al., 2000). Specific objectives of this study were to: (1) survey *T. lintearius* populations for co-occurring potential predators, (2) measure reproductive performance and development of the most abundant natural enemies when held with *T. lintearius* under laboratory conditions and, (3) quantify biological control interference by exclusion of predators from field-released populations of *T. lintearius*.

2. Materials and methods

2.1. Predator survey

Surveys for natural enemies of *T. lintearius* were performed at six sites in western Oregon: Astoria, Baker Beach, Bandon, Clackamas, Elk River, and Sutherlin (Table 1). Sites were selected because *T. lintearius* populations were established at each site for approximately 4 years and these represented the geographical range of *T. lintearius* in Oregon. Monthly surveys were performed at Baker Beach, Bandon, and Sutherlin from March 1998 through March 1999 and single surveys were conducted at the remaining sites (Table 1). Surveys consisted of sampling *U. europaeus* foliage every 10 m along a randomly selected 100-m transect. A total of 20 samples were collected from each transect by excising two *U. europaeus* terminal branches of ca. 25 cm in length. Each sample was sealed in a polyethylene bag, transported to the laboratory, and branches were individually washed to extract arthropods within 48 h. The extraction method entailed placing individual *U. europaeus* branches in separate 1-L jars and adding 300 ml of 70% ethanol (Pratt and Croft, 2000; Zacharda et al., 1988). Lids were placed on jars, shaken manually for 30 s, left to rest for 1 min, and then shaken again for 30 s. Plant material in jars was removed with forceps and slowly rinsed with 70% ethanol over jars. The ethanol and associated contents were poured into a Whatman #4 filter paper funnel, gravity filtrated, and then scanned under a binocular microscope at 40× magnification. All predatory mites washed from branches were mounted on glass slides in Hoyer's medium and identified according to morphological characters (Schuster and Pritchard, 1963). All other predaceous arthropods were

Table 1
Survey sites for predators associated with *Tetranychus lintearius*, a biological control agent of *Ulex europaeus*

Site name	Geographic location ^a	GPS coordinates ^b	Release date ^c	Survey frequency
Astoria	Northern coastal	46.2783N 123.9970W	8/18/94	April 4, 1998
Baker beach	Central coastal	44.0915N 124.1158W	7/20/94	Monthly
Bandon	Southern coastal	43.0543N 124.4083W	9/20/94	Monthly
Clackamas	Northern inland	45.2391N 122.4268W	9/2/94	September 5, 1998
Elk river	Southern coastal	42.7648N 124.4626W	7/19/94	July 28, 1998
Sutherlin	Central inland	43.3970N 123.2974W	8/18/94	Monthly

^a Geographical location of the research sites in western Oregon, coastal: <5 km from ocean; inland: >60 km from ocean.

^b Global positioning system in decimal degrees.

^c Release date of *Tetranychus lintearius* at each site.

preserved in 70% ethanol and identified by taxonomists at the Insect Identification Clinic at Oregon State University or Oregon Department of Agriculture. The number of *T. lintearius* individuals that were washed from plants were also recorded.

2.2. Predaceous mite cultures

Laboratory cultures of *Amblyseius andersoni* Chant, *Galendromus occidentalis* (Nesbitt), *Neoseiulus fallacis* (Garman), and *Typhlodromus pyri* Scheuten were originally collected from agricultural crops in the Willamette Valley, Oregon (Hadam et al., 1986). Cultures had been maintained for 6 years with yearly additions from field-collected mites. These predatory mite cultures were fed mixed life stages of *Tetranychus urticae* (Koch) three times per week before the study period.

Two strains (or source populations) of *Phytoseiulus persimilis* Athias–Henriot (Acari: Phytoseiidae), were also compared. A culture that had historically been maintained on *T. urticae*, PP1, was initiated from individuals provided by Biohelp (BIOHELP OGE-Nützlingszucht, Kapleigasse 16, A-1110 Vienna, Austria). The second strain, PP2, was collected from *T. lintearius* colonies at the Bandon site (Table 1). To adjust for potential preconditioning of metabolic functions or experience gained from having been reared on a specific diet, both strains were divided into two cultures according to prey species used for short-term maintenance: PP1tu and PP2tu were fed *T. urticae* while PP1tl and PP2tl were fed *T. lintearius*. As before, cultures were fed mixed life stages of prey three times per week and maintained for ca. 1 month prior to conducting feeding tests.

All mite cultures were held at $25 \pm 5^\circ\text{C}$, 16:8 L:D (light:dark), and $80 \pm 10\%$ RH (relative humidity). Only randomly selected gravid females were used in this study. Prior to tests, adult female mites were held without food for 24 h to produce similar levels of hunger.

2.3. Predation bioassays

Predation bioassays were conducted on 2.5×2.5 cm arenas constructed of waterproof paper and ringed with a sticky material (Tanglefoot, The Tanglefoot, Grand Rapids MI 49504) to prevent escape by mites (Pratt et al., 1999). Arenas were placed on a piece of water-saturated foam rubber contained in a tray of water (Monetti and Croft, 1997). A single adult female was transferred to each arena with a camel's hair brush. Mixed stages of *T. lintearius* or *T. urticae*, in amounts excess of predator consumption, were provisioned every 24 h and arenas were placed in a 1×2 m environmental chamber at $25 \pm 1^\circ\text{C}$, $80 \pm 10\%$ RH, and 16:8 L:D for 10 days. *T. lintearius* were collected from gorse plants near Florence, Oregon, in September 1998 and *T. urti-*

cae were taken from laboratory cultures reared on *Phaseolus lunatus* L. (Pratt et al., 1998). Survivorship, activity (percent of time spent in ambulation per minute of observation), and oviposition per female per day were assessed every 24 h. Cannibalism was also assessed daily by reviewing each arena for dead or shriveled corpses. To adjust for preconditioning of metabolic functions or experience gained from having been reared on a particular prey species, we did not use data collected during the first three days of the test (Pratt et al., 1999; Van Rijn and Tanigoshi, 1999). For *N. fallacis*, tests were also performed when held with *T. urticae* or no food (starvation) (Pratt et al., 1999). All tests were replicated at least eight times per species (or strain). Means of each measured attribute were calculated and analyzed by general linear models (GLM) and Tukey's HSD procedures.

2.4. Exclusion tests

In the previous two experiments, predatory mites were associated with *T. lintearius* colonies and responded reproductively when held with *T. lintearius* as prey. Although this evidence suggests that predatory mites may be interfering with biological control of gorse, more conclusive evidence can be obtained by using exclusion tests (Goeden and Louda, 1976; Luck et al., 1999). The primary method of excluding phytoseiids from control plots is the application of selective pesticides (Croft, 1990; Lester et al., 1998; Pratt and Croft, 2000). Phytoseiid mites are highly susceptible to synthetic pyrethroids and, although some evidence suggests that spider mites may show increased reproduction and dispersal when exposed to pyrethroids (Helle and Sabelis, 1985; Croft, 1990), recent studies have demonstrated that the tetranychid mite *Oligonychus pratensis* (Banks) and *T. urticae* are not stimulated reproductively by the same active ingredient and application rate that was used herein (Ayyappath et al., 1997). Therefore, we assumed that *T. lintearius* was not reproductively stimulated by the exclusionary pyrethroid application.

Exclusion tests were performed ca. 1 km south of the Bandon study site, the only region where the spider mite specialist *P. persimilis* was recovered. For this test, we selected a continuous, dense, *T. lintearius*-free stand of gorse plants that formed a hedge on the eastern exposure of a road near the site (Table 1). Intermingled gorse foliage in the hedge was ca. 3 m in height, 3 m deep, and extended along the entire 0.5 km of roadway. From this hedge we delineated 12 plots, each measuring 5 m wide. These plots were randomly assigned either applications of a pyrethroid or no spray. Each exclusion plot was sprayed with a 10% field rate of permethrin (Pounce 3.2 EC, 0.03 L/ha) from a pressurized backpack sprayer until runoff on 21 July and 18 August 1999. The remaining plots were treated with water (Pratt and Croft,

Table 2
Predaceous species collected from *Ulex europaeus* during 1998–1999 surveys

Family	Species	Location(s)	Life style type ^a
Phytoseiidae	<i>Amblyseius andersoni</i>	Baker beach	III
	<i>Neoseiulus fallacis</i>	Baker beach	II
	<i>Typhlodromus pyri</i>	Sutherlin	III
	<i>Typhlodromus graminis</i>	Astoria	III
	<i>Typhlodromus arboreus</i>	Baker beach, Bandon	III
	<i>Phytoseiulus persimilis</i>	Bandon	I
	<i>Galendromus occidentalis</i>	Clackamas	II
	<i>Stethorus punctillum</i>	Baker beach, Bandon	
Coccinellidae	<i>Stethorus</i> sp.	Baker beach	
Phlaeothripidae		Baker beach, Bandon	
Micryphantidae		Baker beach, Bandon, Sutherlin	
Bdellidae		Baker beach, Bandon	

^a After McMurtry and Croft (1997): type I, specialized predators of *Tetranychus* species; type II, selective predators of tetranychid mites, particularly with those that produce copious webbing; type III, generalist predators.

2000). To ensure that each plot contained similar levels of spider mites and predatory mites, on 21 July ca. 500 *T. lintearius* and 20 *P. persimilis* adult females were collected from the Bandon study site and inoculated into the center of each plot after the pyrethroid or water application dried on the gorse foliage.

On 21 September 1999 we assessed the presence of active gorse spider mites, the number of spider mite colonies (as delineated by webbing patterns), estimated the number of spider mites, colony size, and number of branches infested with *T. lintearius* for each plot. Individuals of *T. lintearius* aggregate into dense clumps (Millar, 1993), making accurate spider mite counts difficult. Therefore, spider mite densities per plot were estimated by subsampling individuals from a 2-cm³ sampled area and multiplying this value by the area occupied by all spider mite aggregates within each plot. Colony size was estimated by measuring the length, width, and depth of each discrete webbed colony and calculating the volume of mites within each plot. In addition, we measured the relative density of *P. persimilis* by scanning *T. lintearius* colonies or gorse foliage for 10 min with a 10× optical visor (Pratt et al., 1998). Data were $\log(x + 1)$ transformed and, except for comparisons of successful colonization, data means were analyzed with individual Student's *t* tests to distinguish differences among treatments. To compare the continued presence of spider mite colonies among treatments, we used a binomial test with the null hypothesis frequency of 0.5 (SPSS, 1999). For all tests, a *P*-value < 0.05 was considered significant evidence for rejecting the null hypothesis.

3. Results

3.1. Predator survey

Of the predatory arthropods surveyed at the six study sites, 75% belonged to the predatory mite family Phy-

toseiidae (Table 2). When summed among all sites and dates, phytoseiids occupied 39.9% of the 193 randomly sampled *T. lintearius* colonies. The remaining predators belonged to the Phlaeothripidae (20%), Coccinellidae (2%), Micryphantidae (Araneae; 2%), and Bdellidae (1%). The slope of the rarefaction curve after 12 months of sampling approached 0, suggesting that the probability of collecting new species with continued sampling was minimal (Fig. 1; Magurran, 1988).

Among the Phytoseiidae, 57% of the species were generalists (type III), which feed on various mites, insects, and pollens (Table 2; Croft et al., 1998; McMurtry and Croft, 1997). These generalist predators were also the dominant species (most abundant) at five of the six survey sites. The only dominant specialist predator of spider mite species collected was the introduced species *P. persimilis* (McMurtry et al., 1978), which was only collected from the Bandon site.

3.2. Predation bioassays

Survivorship was different between the five phytoseiids tested ($F = 37.47$; $df = 11, 98$; $P < 0.0001$). Lowest levels of survivorship were among the generalist predators *A. andersoni* and *T. pyri* (Table 3). Survivorship of

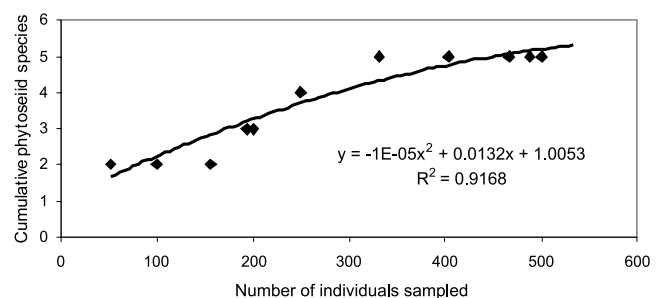


Fig. 1. Rarefaction curve for predatory mite species collected from *Ulex europaeus* during a 1998–1999 survey.

Table 3

Survival, activity, and oviposition of *Neoseiulus fallacis*, *Galendromus occidentalis*, *Typhlodromus pyri*, *Amblyseius andersoni*, and two strains of *Phytoseiulus persimilis* when held with unlimited numbers of different prey during 7 days

Predator mite	Prey species	N	Survivorship ^a	Activity ^b	Egg/female/day ^c
<i>Amblyseius andersoni</i>	<i>T. lintearius</i>	8	0.85 (0.07) b ^f	0.35 (0.03) bc	0.51 (0.05) a
<i>Typhlodromus pyri</i>	<i>T. lintearius</i>	8	0.71 (0.06) bc	0.14 (0.04) ab	0.66 (0.10) a
<i>Neoseiulus fallacis</i>	<i>T. lintearius</i>	8	0.94 (0.03) ab	0.22 (0.04) ab	2.00 (0.06) b
	<i>T. urticae</i>	8	1.00 (0.01) a	0.17 (0.04) ab	1.78 (0.14) b
	Starvation	8	0.36 (0.03) d	0.57 (0.05) c	0.04 (0.03) a
	<i>T. lintearius</i>	8	1.01 (0.05) a	0.34 (0.05) bc	2.89 (0.34) d
<i>Galendromus occidentalis</i>	<i>T. urticae</i>	10	1.00 (0.00) a	0.03 (0.02) a	4.10 (0.06) e
<i>Phytoseiulus persimilis</i> (PP1tu) ^d	<i>T. lintearius</i>	10	0.96 (0.03) ab	0.14 (0.06) ab	3.39 (0.21) d
<i>Phytoseiulus persimilis</i> (PP2tu)	<i>T. urticae</i>	10	1.00 (0.00) a	0.07 (0.02) a	2.83 (0.09) d
<i>Phytoseiulus persimilis</i> (PP2tl)	<i>T. lintearius</i>	10	0.99 (0.01) a	0.13 (0.06) ab	4.17 (0.08) e
P-value ^e			<0.0001	<0.0001	<0.0001

^a Female survival after 7 days in arenas, mean (\pm SE).

^b Female activity (ambulation) within arena per 1 min observation per day.

^c Average number of eggs produced per female per day.

^d *P. persimilis* strains: PP1, commercially available source; PP2, collected from *T. lintearius* colonies at the Bandon site. PP1tu and PP2tu were reared on *T. urticae* prior to the experiment while PP1tl and PP2tl were reared on *T. lintearius*.

^e Means of all tests were analyzed simultaneously by ANOVA, df = 3,28.

^f Means followed by different letters are significant at $\alpha = 0.05$ (Tukey's HSD).

N. fallacis was not different when held with either *Tetranychus* prey species but was much lower when held without food. Similarly, no differences in survivorship were found among the *G. occidentalis* or *P. persimilis* strains, regardless of the tetranychid prey species.

Activity of the predatory mites within the arena was also different among the five species tested ($F = 9.83$; df = 11, 98; $P < 0.0001$). With few exceptions, activity levels demonstrated an inverse trend relative to survivorship: low activity was observed among the specialist predators and highest for generalist predators of tetranychids (Table 3). Activity of *N. fallacis* females was not different between *Tetranychus* prey but significantly higher than when held without food. Again, no differences were found among *P. persimilis* strains.

Egg production differed among the species and strains tested ($F = 83.26$; df = 11, 98; $P < 0.0001$). Oviposition rates were lower for *A. andersoni* and *T. pyri* than other species. Egg production for *N. fallacis* was not different when held separately with *T. urticae* and *T. lintearius* prey but was lower when this species was held without food. *N. fallacis* laid fewer eggs per female per day when held with either *Tetranychus* species than did *G. occidentalis* or *P. persimilis* strains. Significant differences were also found between oviposition rates of the *P. persimilis* strains. Despite preconditioning, the PP1 strain had higher egg production when held with *T. urticae* than with *T. lintearius*. In contrast, the PP2 strain collected from gorse spider mite colonies in Bandon had higher oviposition rates when with *T. lintearius* versus *T. urticae*. Egg production was similar when two *P. persimilis* strains were held with the prey species with which they originally were associated (PP1 on *T. urticae* and PP2 on *T. lintearius*, respectively; Table 3).

3.3. Exclusion tests

Inoculations of *T. lintearius* into study plots initially resulted in similar levels of colonization in exclusion (pyrethroid) and control treatments ($P = 0.219$). However, both the number of discrete spider mite colonies and the mean colony size were greater in the exclusion treatment versus the control (df = 10, $t = 2.42$, $P = 0.02$; df = 10, $t = 2.65$, $P = 0.01$, respectively; Fig. 2). Similarly, a higher proportion of branches in the exclusion treatment were colonized by *T. lintearius* versus those of the control (df = 10, $t = 2.2$, $P = 0.03$). Mean number of spider mites per treatment also followed a similar trend (df = 10, $t = 1.6$, $P = 0.07$). Population densities of *P. persimilis* approached statistical reductions in exclusion plots when compared to the control (df = 10, $t = 1.73$, $P = 0.06$; Fig. 2d).

4. Discussion

Biotic resistance describes the collective impact of parasites, predators, pathogens, and competitors on the establishment and proliferation of a nonindigenous species (Simberloff and Holle, 1999). Like any biological invasion, these natural control mechanisms can interfere with the establishment and development of high population densities that are considered desirable for classical biological control agents. In most natural systems, for instance, predators are the main contributors to biotic resistance of spider mites (Helle and Sabelis, 1985; Peterson, 1993; Walter, 1999; Walter and Proctor, 1999). Surveys aimed at determining if natural enemies were becoming associated with *T. lintearius* and interfering with the suppression of *U. europaeus* in Oregon resulted

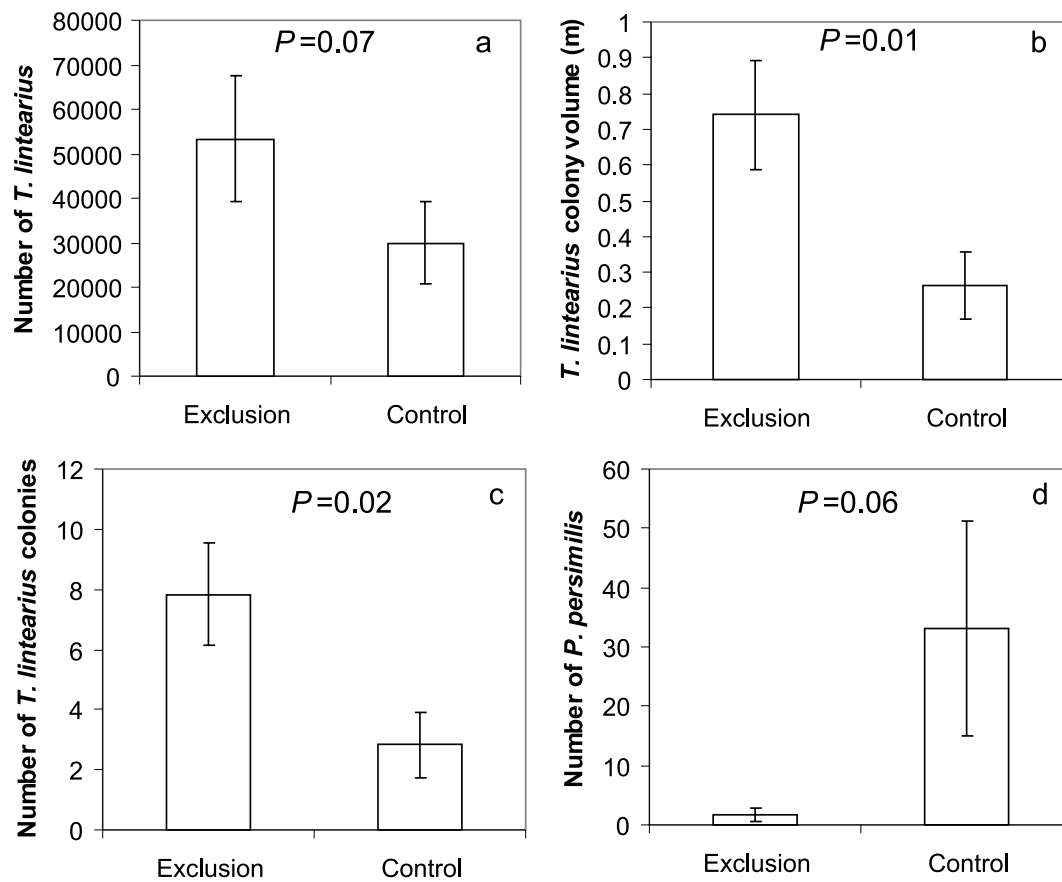


Fig. 2. Density and colony size estimates (\pm SE bars) for the weed biological control agent *Tetranychus lintearius* after the predatory mite *Phytoseiulus persimilis* was excluded from gorse (*Ulex europaeus*) plants.

in the discovery of various predaceous arthropods, the most common being predatory mites in the family Phytoseiidae (Table 2). Among all of the phytoseiid species that were collected, the most abundant predators were classified as generalists that feed on a wide range of diets including insects, pollen, spider mites, and other mites (McMurtry and Croft, 1997). At the Bandon site, however, the specialized predator of *Tetranychus* species, *P. persimilis* was the most common natural enemy associated with the biological control agent. In general, these findings suggest that *T. lintearius* has acquired generalist and specialist predatory mites, but association alone is not sufficient evidence to conclude that these natural enemies are negatively affecting the biological control agent.

Evaluating the abilities of these predatory mites to survive and reproduce when held with *T. lintearius* lends additional evidence to the interference hypothesis. Results from predation bioassays suggest that all phytoseiids tested could feed and survive on *T. lintearius*. Not surprisingly, the more specialized spider mite predators had higher rates of survival, generally lower activity (indicating colonization and arrestment), and higher reproduction when held with *T. lintearius* than

the generalists. The specialist *P. persimilis*, for instance, oviposited >4 eggs per day versus 0.51 for the generalist *A. andersoni* (Table 3). When comparing ovipositional rates among *P. persimilis* strains, those collected from *T. lintearius*-infested gorse plants oviposited more eggs per day when held with *T. lintearius* than with the congener *T. urticae*, even after a 30-day preconditioning period with the other respective prey species. These findings suggest that the *P. persimilis* strain collected from the *T. lintearius* colonies has increased its propensity (specialization) to feed on the weed biological control agent.

To quantify impacts, and more conclusively to determine if predatory mites were interfering with biological control (Goeden and Louda, 1976; Luck et al., 1999), we excluded *P. persimilis* from replicated plots of *T. lintearius*-infested gorse plants. The number of colonies and volume of gorse foliage colonized were higher when *P. persimilis* was excluded from plots (Fig. 2). In addition to co-occurring with and preying upon the gorse spider mite, *P. persimilis*, and most likely the other phytoseiids as well, are limiting the densities of *T. lintearius*. Although we have evidence that these phytoseiids are suppressing *T. lintearius*, it remains unclear what level of spider mite density is needed to reduce the

competitive superiority of *U. europaeus*. Are the biological control agents inflicting sublethal effects on the plant regardless of the suppressive effects of the phytoseiids? Post-release evaluations on the density-dependent impacts of *T. lintearius* on *U. europaeus* are needed to accurately quantify the role predatory mites play in the interference of biological control of gorse.

As described earlier, four years after establishment of *T. lintearius*, spider mite population levels were high, spreading and inflicting severe localized damage to *U. europaeus* plants. During this study (1998–1999), spider mite populations decreased in all locations, although none as dramatically as in the Bandon site. The apparent dissimilarities among biological control agent population levels in New Zealand versus the Bandon site seemed to be less pronounced by 1999 than in earlier years. In Oregon, a distinct lag period appears to have occurred before predators exerted a detectable impact on *T. lintearius* populations (1994–1998), consistent with the acquisition phase reported for other introduced species (Goeden and Louda, 1976; Hill and Hulley, 1995). Explanations for this lag phase may be related to rates of population increase of initially rare phytoseiids.

Specialist predatory mites are often selected for biological control of spider mite pests in agricultural or horticultural systems because of their ability to functionally and numerically respond to outbreaks of pest mites (McMurtry and Croft, 1997). In contrast, the most common predatory mites found in natural systems are generalists and often these types of species regulate spider mite populations in unmanaged habitats (McMurtry, 1992). Therefore, which predatory type causes the greatest interference to the biological control of gorse? One explanation may be related to spider mite population dynamics, which differ among predation types. Specialist predatory mites, for instance, are arrested in prey patches longer, resulting in lower rates of dispersal and destruction of additional prey patches (Pratt et al., 1998). Nearby prey patches, in the absence of the predator, may reach high, damaging densities prior to the arrival of the specialist natural enemy. This type of interaction results in population oscillations characteristic of a “boom and bust” predator–prey relationship. Generalist predatory mites, in contrast, feed on a wide range of prey and are not subject to such volatile interactions, leading some to suggest that generalists are largely responsible for low-level pest regulation (McMurtry, 1992). Often, specialist and generalist types of predaceous mites act in combination or in a sequence, with specialists responding quickly, suppressing spider mite densities and subsequently being out-competed by generalist phytoseiids that regulate spider mites thereafter (McMurtry and Croft, 1997). Such combined actions are expected to occur at the Bandon site after more complete decimation of spider mites was accomplished by *P. persimilis*.

Because phytoseiids, and specifically *P. persimilis*, pose a potential threat to successful biological control of gorse, possible management actions may be used to reduce regional impacts on *T. lintearius* colonies. Firstly, redistribution of predator contaminated spider mite colonies should be terminated. This tactic has immediate relevance as other US states and countries begin efforts to introduce *T. lintearius* into gorse-infested habitats. An additional tactic may include use of selective pesticides, like the pyrethroid used herein, which inflicted high mortality on the phytoseiid but has little if any negative effect on the biological control agent (Croft, 1990). This technique has been used to enhance biological control of prickly pear (*Opuntia megacantha* Salm-Dyck) by applying selective pesticides to populations of the biological control agent *Dactylopius opuntiae* (Cockerell) (Homoptera: Dactylopiidae), a DDT-resistant cochineal and resulted in concomitant destruction of its coccinellid predators (Annecke et al., 1969). This tactic may be theoretically feasible but nontarget risks to the surrounding biota and economics limit the practicality of large-scale, chemically based methods of suppressing predators in gorse dominated regions of western Oregon.

Although less commonly reported than other taxa, this is not the first incident of a mite interfering with the establishment or impact of a weed biological control agent. Poor establishment rates of the chrysomelid flea beetle *Altica carduorum* Guer. (Coleoptera: Chrysomelidae), for instance, were attributed to predation of eggs and larvae by erythraeid mites, specifically those in the genera *Erythraeus*, *Leptus*, and *Sphaerolophus* (Peschken et al., 1970). In Australia, biological control of *O. megacantha* was negatively impacted when the endophytic larvae of *Cactoblastis cactorum* Bergroth (Lepidoptera: Pyralidae) were preyed upon by various arthropods, including predatory mites in the genus *Micromaris* (Acari: Erythraeidae) (Dodd, 1940).

Our results also have relevance to the classification of predation types among phytoseiid mites. Assuming ovipositional rates indicate feeding specialization (Dicke et al., 1990; Pratt et al., 1999), *P. persimilis* (when held with the optimal prey) appears to be the most specialized predator of *T. lintearius* tested herein, with *N. fallacis* and *G. occidentalis* demonstrating intermediate levels of reproduction, while *A. andersoni* and *T. pyri* had the lowest. The ranking of specialization among these mites is consistent with those predicted by McMurtry and Croft (1997, as presented in Table 2). Additionally, the heightened specialization of strains of *P. persimilis* between the two different *Tetranychus* species was surprising. These mites are specialists of *Tetranychus* species but, to our knowledge, this is the first report of strain specialization of *P. persimilis* in feeding preference within the spider mite genus.

Acknowledgments

We thank R. Hill, J.A. McMurtry, P.B. McEvoy, and two anonymous reviewers for comments on the manuscript. We thank J.A. McMurtry for assistance with identification of mites. This research was funded in part by a grant from the Oregon Department of Agriculture.

References

- Annecke, D.P., Karny, M., Burger, W.A., 1969. Improved biological control of prickly pear, *Opuntia megacantha* Salm-Dyck, in South Africa through the use of an insecticide. *Phytophylactia* 1, 9–13.
- Ayyappath, R., Witkowski, J.F., Higley, L.G., 1997. Ovipositional responses of two species of spider mites to sublethal concentrations of permethrin and methyl parathion on corn. *Environ. Entomol.* 26, 489–496.
- Beirne, B.P., 1975. Biological control attempts by introductions against pest insects in the field in Canada. *Can. Entomol.* 107, 225–236.
- Croft, B.A., 1990. *Arthropod Biological Control Agents and Pesticides*. Wiley, New York.
- Croft, B.A., Monetti, L.N., Pratt, P.D., 1998. Comparative life histories and predation types: are *Neoseiulus californicus* and *N. fallacis* similar type II selective predators of spider mites. *Environ. Entomol.* 27, 531–538.
- Dicke, M., Sabelis, M.W., Jong, M.D., Alers, M.P.T., 1990. Do phytoseiid mites select the best prey species in terms of reproductive success? *Exp. Appl. Acarol.* 8, 161–173.
- Dodd, A.P., 1940. *The Biological Campaign Against Prickly Pear*. Commonwealth Prickly Pear Board, Brisbane.
- Fisher, T.W., Andres, L.A., 1999. Quarantine: Concepts, facilities, and procedures. In: Bellows, T.S., Fisher, T.W. (Eds.), *Handbook of Biological Control*. Academic Press, San Diego, pp. 103–124.
- Goeden, R.D., Louda, S.M., 1976. Biotic interference with insects imported for weed control. *Annu. Rev. Entomol.* 21, 325–342.
- Hadam, J.J., Aliniaze, M.T., Croft, B.A., 1986. Phytoseiid mites of major crops in Willamette Valley, Oregon, and pesticide resistance in *Typhlodromus pyri*. *Environ. Entomol.* 15, 1255–1263.
- Helle, W., Sabelis, M.W., 1985. In: *Spider Mites: Their Biology, Natural Enemies and Control*, vol. 1B. Elsevier, Amsterdam.
- Hill, R.L., Grindell, J.M., Winks, C.J., Sheat, J.J., Hayes, L.M., 1991. Establishment of gorse spider mite as a control agent for gorse. *Proc. N. Z. Weed and Pest Control Conf.* 44, 31–34.
- Hill, M.P., Hulley, P.E., 1995. Host-range extension by native parasitoids to weed biocontrol agents introduced to South Africa. *Biol. Control* 5, 297–302.
- Hill, R.L., Stone, C., 1985. Spider mites as control agents for weeds. In: Helle, W., Sabelis, M.W. (Eds.), *Spider Mites: Their Biology, Natural Enemies and Control*, vol. 1B. Elsevier, Amsterdam, pp. 443–448.
- Lester, P.J., Thistlewood, H.M.A., Harmsen, R., 1998. The effects of refuge size and number on acarine predator–prey dynamics in a pesticide-disturbed apple orchard. *J. Appl. Ecol.* 35, 323–331.
- Luck, R.F., Shepard, B.M., Kenmore, P.E., 1999. Evaluation of biological control with experimental methods. In: Bellows, T.S., Fisher, T.W. (Eds.), *Handbook of Biological Control*. Academic Press, San Diego, pp. 225–242.
- Magurran, A.E., 1988. *Ecological Diversity and its Measurement*. Princeton University Press, New Jersey.
- McEvoy, P.B., Coombs, E.M., 1999. Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecol. Appl.* 9, 387–401.
- McMurtry, J.A., 1992. Dynamics and potential impact of ‘generalist’ phytoseiids in agroecosystems and possibilities for establishment of exotic species. *Exp. Appl. Acarol.* 14, 371–382.
- McMurtry, J.A., Croft, B.A., 1997. Life-styles of phytoseiid mites and their roles in biological control. *Annu. Rev. Entomol.* 42, 291–321.
- McMurtry, J.A., Oatman, E.R., Phillips, P.A., Wood, C.W., 1978. Establishment of *Phytoseiulus persimilis* (Acari: Phytoseiidae) in southern California. *Entomophaga* 23, 175–179.
- Millar, G.F., 1993. Aggregation and development of the gorse spider mite *Tetranychus lintearius* Dufor (Acari: Tetranychidae). Masters Thesis, University of Canterbury, Christchurch.
- Monetti, L.N., Croft, B.A., 1997. *Neoseiulus californicus* and *Neoseiulus fallacis*: larval responses to prey and humidity, nymphal feeding drive, and nymphal predation on phytoseiid eggs. *Exp. Appl. Acarol.* 21, 225–234.
- Peschken, D., Friesen, H.A., Tonks, N.V., Banham, F.L., 1970. Releases of *Altica carduorum* against the weed Canada thistle (*Cirsium arvense*) in Canada. *Can. Entomol.* 102, 264–271.
- Peterson, P.G., 1993. The potential ability of *Stethorus bifidus* (Kapur) to regulate populations of *Tetranychus lintearius* (Dufor). Masters Thesis, Massey University, Auckland, New Zealand.
- Peterson, P.G., McGregor, P.G., Springett, B.P., 1994. Development of *Stethorus bifidus* in relation to temperature: implications for regulation of gorse spider mite populations. *Proc. N. Z. Plant Prot. Conf.* 47, 103–106.
- Pratt, P.D., Croft, B.A., 2000. Overwintering and comparative sampling of *Neoseiulus fallacis* (Acari: Phytoseiidae) on ornamental nursery plants. *Environ. Entomol.* 29, 1034–1040.
- Pratt, P.D., Monetti, L.N., Croft, B.A., 1998. Within- and between-plant dispersal and distributions of *Neoseiulus californicus* and *N. fallacis* in simulated bean and apple branch systems. *Environ. Entomol.* 27, 148–153.
- Pratt, P.D., Schausberger, P., Croft, B.A., 1999. Prey-food types of *Neoseiulus fallacis* and literature versus experimentally derived prey-food estimates for five phytoseiid species. *Exp. Appl. Acarol.* 23, 551–565.
- Rees, M., Hill, R.L., 2001. Large-scale disturbances, biological control and the dynamics of gorse populations. *J. Appl. Ecol.* 38, 364–377.
- Rees, N.E., Piper, G.L., Quimby, P.C., Jr., Coombs, E.M., Turner, C.E., Spencer, N.R., Knutson, L.V., 1996. *Biological Control of Weeds in the West*. Western Society of Weed Science, Bozeman.
- Schuster, R.O., Pritchard, A.E., 1963. Phytoseiid mites of California. *Hillgardia* 34, 191–194.
- Simberloff, D., Holle, B.V., 1999. Positive interactions of nonindigenous species: invasional meltdown. *Biol. Invasions* 1, 21–32.
- SPSS 1999. *SPSS Base 10.0 Application Guide*. SPSS, Chicago, IL.
- Van der Geest, L., Elliot, S.L., Breeuwer, J., Beerling, E., 2000. Diseases of mites. *Exp. Appl. Acarol.* 24, 497–560.
- VanRijn, P.C.J., Tanigoshi, L.K., 1999. Pollen as food for the predatory mites *Iphiseius degenerans* and *Neoseiulus cucumeris* (Acari : Phytoseiidae): dietary range and life history. *Exp. Appl. Acarol.* 23, 785–802.
- Walter, D.E., 1999. Cryptic inhabitants of a noxious weed: Mites (Arachnida:Acari) on *Lantana camara* L. invading forests in Queensland. *Aust. J. Entomol.* 38, 197–200.
- Walter, D.E., Proctor, H.C., 1999. *Mites: Ecology, Evolution and Behaviour*. CABI, Wallingford, Oxon, UK.
- Zacharda, M., Pultar, O., Muska, J., 1988. Washing technique for monitoring mites in apple orchards. *Exp. Appl. Acarol.* 5, 181–183.